Studies on the Population Ecology of the Salt Marsh Gastropod

Batillaria zonalis

BY

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(6 Text figures)

INTRODUCTION

AMONG THE MOST IMPORTANT parameters of stability within any ecological community are demographic characteristics of component species populations. In attempting to explain community dynamics, therefore, information on the individual life histories of animals living in the community must be made available. Life history patterns reflect evolved characteristics concerned with the ability of a species to persist in a given environment. In the present study, aspects of the life history of the salt marsh gastropod *Batillaria zonalis* (Bruguière, 1792) have been investigated for a period of 2 years. Trends in population dynamics and aspects of its biology in 2 salt marsh localities in Tomales Bay, California, are described. The results of this study are discussed within the context of population stability in salt marsh communities.

Batillaria zonalis, the only representative of the genus found on the California coast of North America, is presently known to occur from Boundary Bay, British Columbia, Canada, to Elkhorn Slough, central California (HANNA, 1966). *Batillaria zonalis* is native to Japan and BARRETT (1963) suggests that the snail was probably introduced into Tomales Bay as early as 1928 when the first sets of the oyster *Crassostrea gigas* (Thunberg, 1793) were planted in the bay. BONNOT (1935), however, was first to observe the snail along the coast of California. Although *B. zonalis* is very abundant in several localities throughout its range, the only ecological investigation of the species is MACDONALD'S (1967) survey of populations of 3 salt marshes along the California coast.

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HABITAT

Tomales Bay is a drown rift valley located approximately 64 km north of San Francisco, California. The Walker Creek salt marsh is located at the mouth of Walker Creek 4.2 km from the mouth of the bay. The Millerton marsh, located south of Millerton Point, is 18.4 km from the mouth of the bay. Comparative studies of historic maps and aerial photographs confirm a recent origin for both marshes. Maps published in 1861 show the present sites of the marshes as subtidal mudflats. The accretion of sediment can be traced to agricultural practices introduced in the mid-nineteenth century (DAETWYLER, 1965).

MACDONALD (1967) noted a characteristic vertical zonation pattern occurring in Pacific coast salt marshes where the lower limit of salt marsh vegetation approximates the mean lower low water (MLLW) level. Using this observation, he divided each marsh into 2 main sub-environments. The first, where tidal submergences frequently last longer than 6 hours and are never separated by more than 15 days, extends from the lower limit of marsh vegetation to MHHW. The second division includes the vertical zone between MHHW and EHW where short tidal submergences on several consecutive days are followed by several weeks of continuous exposure. Approximately 85% of the total area of the 2 Tomales Bay marshes is above the MHHW level.

Using MACDONALD'S (1967) general classification, areas for sampling *Batillaria zonalis* were subdivided as follows:

A.   Marsh pans – depressions on the marsh surface covered by water on an outgoing tide.

B.   Tidal Creeks – channels bisecting the surface of the marsh.

C. Mudflat areas – areas completely drained of water on an ebb tide.

D. Vegetation zones – areas below MHHW where *Salicornia pacifica* is present.

After preliminary sampling of *Batillaria zonalis,* 2 major habitats (pans and creeks) existing on the marshes were sampled over a period of 18 months. Three pans were sampled at each marsh. The pans are approximately 3 to 5 cm in depth, surrounded by *Salicornia pacifica.* The pans vary in dimension; the largest is about 15 m long and 3 m wide, while the smallest is 2 m long and $1\frac{1}{2}$ m wide. Two sampling areas at Walker Creek and 3 at Millerton are tidal creeks.

Temperature of the upper substrate and standing water in the different sampling areas is quite variable at both salt marshes. Measurements taken December 1970, October 1971, and March 1972, show a variation of at least 5° C between stations at each marsh. A daily temperature cycle, however, is evident in the marshes with the highest temperature occurring in mid-afternoon. The highest seasonal temperatures were recorded in July and August 1971 (29° C), and the lowest were noted in January 1972 (1° C).

Climatological information from the Pacific Marine Station, Dillon Beach, provides monthly rainfall and temperature records that approximate weather conditions in Tomales Bay. Weather data from December 1970 to June 1972 indicate no unusual variation in temperature when compared to a 4-year monthly average, while rainfall was below normal.

MATERIALS AND METHODS

After a preliminary sampling survey in December 1970, changes in the abundance of *Batillaria zonalis* in the 2 salt marshes were studied by periodic sampling of selected study areas. Samples were obtained with a coring tube 10.16 cm in diameter and 12 cm long. Twenty random sampling coordinates were located in each study area for each sampling date. The core was pushed into the substrate to a depth of 4 to 5 cm and the sediment was removed. Since the snails are normally found on the surface of the substrate, these depths were adequate. In winter months, the snails burrowed below the surface but were always found in the upper 2 cm of the sediment. Core samples were wet-sieved in the field, using a 1 mm screen.

The snails were measured from the tip of the siphonal canal to the apex of the shell with vernier calipers. After the snails were counted and measured, they were returned

to their respective sampling areas. At various times during the study it was necessary to bring samples to the laboratory for marking. The samples were always returned to the marsh study areas within 24 hours of collection.

RESULTS

General Distribution of *Batillaria zonalis*

In a general survey of the Walker Creek and Millerton salt marshes in December 1970, the distribution of *Batillaria zonalis* was found to coincide with the lower limit of salt marsh vegetation. The abundance of the snails greatly diminished above MHHW. Analysis of samples obtained in January 1971 from the 4 types of habitats described in the Habitat section, are presented in Table 1. The results are expressed as a frequency index (the portion of the total number of samples in which the snails were present) and in terms of absolute abundance. The frequency index is dependent upon snail density and dispersion pattern, and any tendency toward aggregation results in an underrepresentation of the values. The abundance of *B. zonalis* follows a consistent pattern at both salt marshes with greatest densities occurring in marsh pans and creeks and lowest densities in mudflats and vegetation zones.

Table 1

Absolute abundance (numbers/m²) and frequency indices of *Batillaria zonalis,* January 1971

Locality	Abundance	Frequency Index
Walker Creek		
Marsh Ponds	104.9	0.70
Tidal Creeks	86.4	0.54
Mudflats	1.2	0.06
Vegetation Zones	0.0	0.00
Millerton		
Marsh Ponds	76.5	0.56
Tidal Creeks	61.7	0.58
Mudflats	0.6	0.02
Vegetation Zones	0.0	0.00

Probably the major factor affecting the distribution of *Batillaria zonalis* is the length of time which the snails are exposed to atmospheric conditions. In marsh pans, the snails are covered by a thin layer of water even on low tides, and in the tidal creeks the snails are normally covered by water at least once every 12 hours. The vege-

tation zones and mudflat areas, on the other hand, are characterized by shorter periods of submergence and longer periods of exposure. Another factor affecting the snail distribution may be the characteristics of the marsh substrate. *Batillaria zonalis,* a deposit feeder that ingests large amounts of benthic diatoms (WHITLATCH, 1972), may congregate in areas of high diatom population density.

Growth

Comparisons of the annual growth rates of *Batillaria zonalis* were studied to estimate the age of the snails at the 2 salt marshes. WILBUR & OWENS (1967) have reviewed methods of measuring growth in mollusks and the procedures commonly applied to gastropod populations are: (1) measuring the distances between successive annuli on the operculum or counting shell annuli; (2) marking measured individual animals and remeasuring at given intervals; (3) following the shifts in size-frequency modes corresponding to different size (age) groups per unit time. Since *B. zonalis* exhibits no annuli on the shell or operculum, the latter 2 methods of estimating growth were used.

Shifts in the Modes of the Size-frequency Distributions

Figure 1 illustrates an example of a size-frequency distribution of *Batillaria zonalis*. The data follow the usual polymodal distribution characteristic of animal populations made up of several distinct age-groups. Juveniles form a well-defined mode at 0.3 cm, first year individuals at 0.7 cm, and second year animals at 1.3 cm. Older snails are insufficient in number to give rise to distinguishable modes.

The mean annual growth of an age-group of organisms can be estimated by plotting the shifts of the modes of size-frequency distributions at one year (L_t) against the modes of the distributions in the next year (L_{t+1}). This is the Ford-Walford plot (Figure 2) described by the equation:

$$L_{t+1} = L_t(1 - e^{-k}) + L_\infty e^{-k}$$

(adjacent column →)

Figure 2

Ford-Walford plot of shell length at time t (L_t) on the abscissa and shell length one year later (L_{t+1}) on the ordinate. ● : data from size-frequency modes in 1971 and 1972 for Walker Creek; ○ : data from size-frequency modes in 1971 and 1972 for Millerton; ▲ : data from mark-recapture experiment at Walker Creek; △ : data from mark-recapture experiment at Millerton

where L_t = length at time t, L_{t+1} = length one year later, L_∞ = theoretical maximum size (represented by an intercept of the Ford-Walford plot with a 45° line), k =
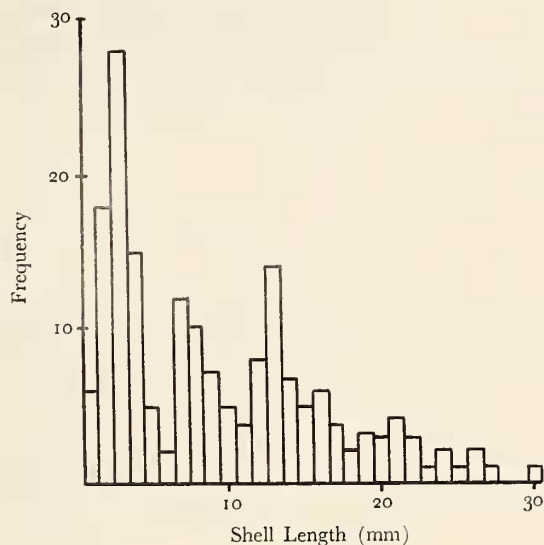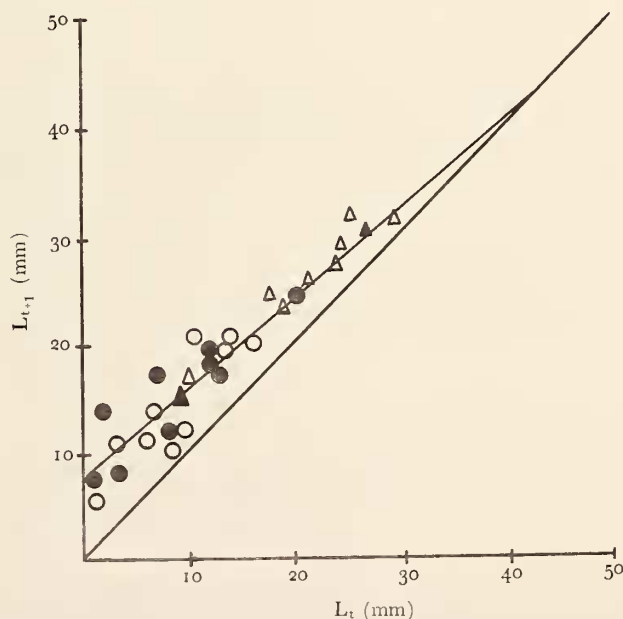

Figure 1

Example of a size-frequency distribution of *Batillaria zonalis*. Data collected July 17, 1971 at Walker Creek

growth rate, and e = base of the natural logarithms (HANCOCK, 1965). The equation was estimated by least squared analysis as:

$$L_{t+1} = 0.7 + 0.8L_t$$

The linear regression analysis resulted in a maximum size of 4.2 cm, though the largest snail found by this investigator was 3.5 cm. KNIGHT (1968) has shown that limited importance should be attached to the L_∞ values.

Marked Individual Animals

In May 1971, approximately 800 snails at each marsh were marked with adhesive tags covered with epoxy resin. The snails were returned to their respective localities and in May 1972, 8 snails from Millerton and 2 snails from Walker Creek were recovered. The shell lengths at the initial time of release (L_t) are plotted against the lengths at recapture (L_{t+1}) in Figure 2. Results of the 2 methods for estimating annual growth in *Batillaria zonalis* are similar, suggesting that the Ford-Walford equation gives a fairly accurate estimate of growth for this species. The Student t test of significance for the differences between

the 2 methods for estimating growth showed: t for differences between slopes = 2.17, p < 0.05; t for differences between heights = 3.67, p < 0.01.

Based on the assumption that young *Batillaria zonalis* settle at 1 mm, Figure 3 shows a conventional growth curve where shell length is plotted against age. The maximum age of the snails was estimated to be 10 years.

Reproduction and Recruitment

Examination of gonad smears in April 1972 showed maturity (motile sperm and fully developed ova) to occur at about 1.3 cm (2 years in age). Figure 4 indicates that the majority of copulating snails observed in the field are greater than 1.5 cm and few individuals less than 1.5 cm
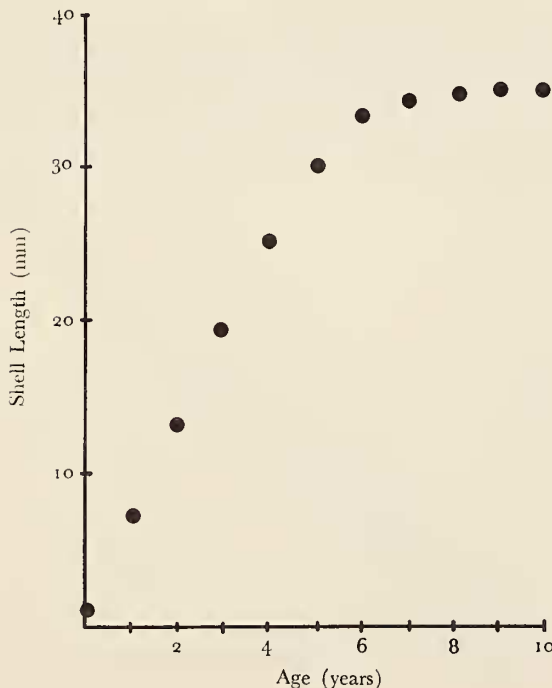

Figure 3

Shell length derived from Ford-Walford equation fitted in Figure 2, plotted against age in years. It is assumed that the juveniles settle at 1.0 mm
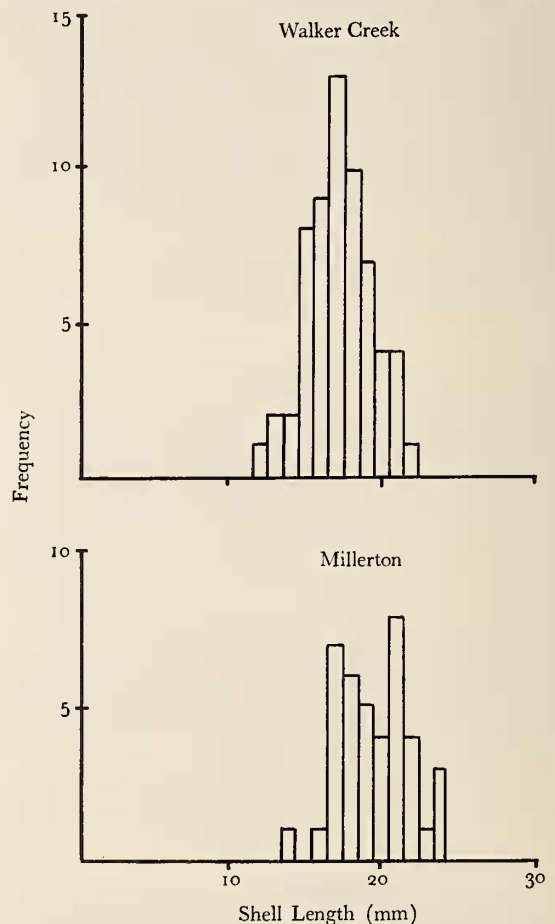

Figure 4

Size-frequency distribution of copulating snails from Walker Creek and Millerton. Data pooled from 4 sampling dates from April to June 1972

were observed to be copulating. In all cases, no first year individuals (0.5 to 1.0 cm) were observed copulating. Comparative analysis of the size-frequency distributions (using Kolmogorov-Smirnov non-parametric statistics) of copulating snails at both marshes showed no differences between sampling periods in the 1972 breeding season and in salt marsh localities. Copulating pairs of *Batillaria zonalis* were observed from March to June in both 1971 and 1972, with greatest numbers occurring in early May. Table 2 gives the number of copulating pairs of snails/m² at the 2 marshes for 1972.

Table 2

Estimates of the abundance (snails/m²) of copulating pairs of *Batillaria zonalis* in 1972 (data pooled from all sampling stations at each marsh)

Walker Creek		Millerton	
March 8, 1972	2.2	March 8, 1972	1.8
March 21, 1972	0.3	March 23, 1972	0.0
April 7, 1972	1.5	April 6, 1972	2.6
May 5, 1972	6.3	May 5, 1972	7.0
May 16, 1972	3.3	May 12, 1972	2.5
June 1, 1972	0.1	June 1, 1972	0.0

Unfortunately, there were few opportunites to determine the exact number of egg masses laid by a single female. Animals did not deposit eggs in the laboratory and only 4 egg strings were found in the field. All the egg strands found were laid in protected pans adhering to *Zostera marina* Linnaeus, 1753, or deposited on the surface of the sediment. In view of the large number of copulating pairs of snails observed at the 2 marshes and the small number of egg masses located, it is possible that attachment to the substrate may not be the general case. Eggs laid on *Z. marina* fragments, for example, could easily be washed away with the tides.

Fertilized eggs are laid in strands 1 to 2 cm long, encased within a sheath composed of sediment and fecal material. The eggs appear white when first deposited and become yellowish as development proceeds. Individual eggs are 0.2 mm in diameter and only one egg occurs in each egg capsule. Analysis of 2 egg strands showed an average of 13 eggs/mm of egg strand. Attempts to culture 2 of the egg masses failed. Habe (1944, in Macdonald, 1967) reports that the veligers settle after a brief planktonic phase.

Settlement of juveniles of *Batillaria zonalis* occurred between June and August in both 1971 and 1972, with the greatest number occurring in late June. Juveniles entered the populations as individuals 1 to 2 mm in length. The average densities of the juveniles at the different sampling stations for June 1972 are given in Table 3. Densities of newly settled individuals are highly variable between sampling localities and settlement occurred only in the marsh pans; no juveniles settled in any of the tidal creek areas.

Table 3

Density estimates of juveniles settling on the Walker Creek and Millerton salt marshes, June 1971. Numbers/10.16 cm core ± 95% confidence limits

Walker Creek		Millerton	
Marsh Pans		Marsh Pans	
Station 1	3.05 ± 1.31	Station 1	9.21 ± 6.25
Station 2	11.21 ± 4.64	Station 2	1.60 ± 1.15
Station 3	0	Station 3	0.45 ± 0.32
Tidal Creeks		Tidal Creeks	
Station 1	0	Station 1	0
Station 2	0	Station 2	0
Station 3	0	Station 3	0

Population Abundance

Comparative analysis of the estimates of population size of *Batillaria zonalis* at the 2 salt marshes shows a great deal of variability between sampling stations. The results, however, indicate a large and relatively stable population size.

Marsh pan localities at Walker Creek showed increases in numbers of snails from May through August 1971, which can be traced to the recruitment of the 1971 age-group of snails (Figure 5). The marsh pans at Millerton show the same general trend (Figure 5) with recruitment also occurring in the summer.

The tidal creek sampling stations at both marshes have a more stable population abundance when compared to the marsh pans (Figure 5). This stability may be the result of the lack of recruitment occurring in the tidal creeks. There was, however, a sharp increase in the number of snails in December 1970 and January 1971, at Walker Creek. Increased amounts of *Ulva* sp. and *Enteromorpha* sp., upon which *Batillaria zonalis* commonly browses, were noted during this period and may explain the sudden
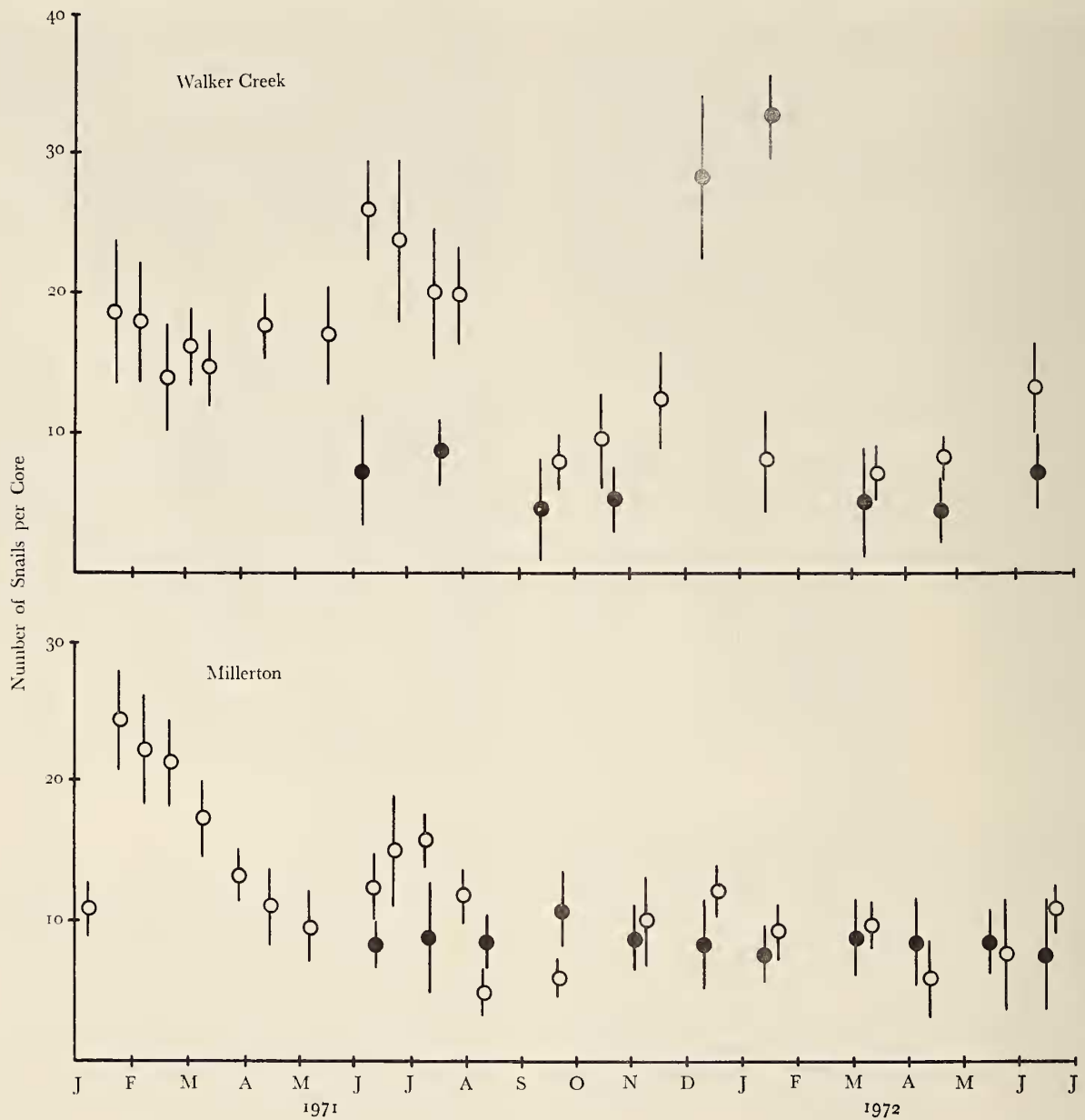
Figure 5

Estimates of the population abundance of *Batillaria zonalis* at
Walker Creek and Millerton showing means and 95% confidence
limits. ● : tidal creek stations; ○ : marsh pan stations.
Averages based upon 10.16 cm cores

population increase. All of the tidal creek stations at Millerton showed remarkable stability in population abundance over the entire sampling period.

Variability in population abundance of the gastropods in the 2 salt marshes may be the result of 2 factors. Firstly, *Batillaria zonalis* is highly mobile. By extending its foot and using the surface tension of the water, the snails have the capability of floating. Individuals were seen floating on incoming tides in the tidal creeks and marsh pans at both marshes. Analysis of mark-recapture experiments in December 1970 and May 1971 indicates that over 75% of the marked snails moved from a one square meter area within 7 days after release. Secondly, experiments concerned with the effects of desiccation on different size groups of snails indicate that individuals less than 0.5 cm are highly sensitive to desiccation (Table 4). Mortality rates due to desiccation will be disproportionately high in smaller snails and abundances of juveniles in areas of the marsh that are commonly exposed for long periods of time (*e. g.,* the vertical zone above the marsh vegetation) would be greatly affected by desiccation and would cause increased population fluctuations.

Table 4

Number and percentage of snails of different size groupings surviving desiccation at three time periods (each experiment initially included 25 animals)

Time in	0.0 - 0.5 cm		0.5 - 1.0 cm		1.0 - 1.5 cm		1.5 + cm	
Hours	No.	%	No.	%	No.	%	No.	%
12	21	84	25	100	25	100	25	100
24	2	8	23	92	25	100	25	100
48	0	0	20	80	24	96	25	100

Predators and Parasites of *Batillaria zonalis*

Although Macdonald (1967) suggests that possible predators of *Batillaria zonalis* might include different species of shore birds, on 9 separate surveys throughout the study no shell fragments were found in bird fecal material collected from the 2 marshes. Other predators of the snails may include crabs, although they were never observed preying upon the snails, and bottom fishes which enter the marsh creeks on incoming tides.

During the course of laboratory observations of *Batillaria zonalis,* infestation of larval trematode parasites were found in the gonads and digestive glands of the snails. Microscopic observations of heavily infected gonads re-

vealed no eggs or sperm. Castration by larval trematode parasites has been reported in the mollusk *Transenella tantilla* (Gould, 1852) (Obrebski, 1968). Some cercariae and rediae were found in the digestive diverticula but were not as abundant as those infesting the gonadal region.

Estimates of the levels of parasitic infestation were obtained from additional samples collected in May 1972. Analysis of *Batillaria zonalis* collected from both salt marshes showed an average of $1\frac{3}{4}\%$ trematode infestation. The length-frequency distributions (Figure 6) of the sampled snails indicate no parasitism evident in snails smaller than 1.5 cm. In a second sampling of both marshes

Figure 6

Size-frequency distribution of 20 random samples of *Batillaria zonalis* collected May 1972 at Walker Creek and Millerton. Snails parasitized by larval trematodes indicated by darkened portion of distribution

in May 1972, only snails greater than 2.0 cm were collected and examined for parasites. From 90 *B. zonalis* examined, 39½% were infected at Walker Creek and 35% were infected at Millerton. Chi-squared analysis showed no significant difference in the infestation levels at the 2 marshes (Chi-squared = 0.272, df 1). All individuals greater than 3.0 cm were infected.

Since samples were only obtained during May 1972, the results must be considered preliminary in nature. The presence of high infestation by trematodes in older snails, however, indicates recruitment may be affected by parasitism. If egg production increases with age, which is common in gastropods (PHILLIPS, 1969), older snails could account for a disproportionate amount of egg production in the populations.

DISCUSSION

Both spatial and temporal physical variability are important characteristics of the salt marsh habitat and impose severe restraints upon species inhabiting them. In the present study, variations in larval recruitment and fluctuations in population density may be the result of local environmental conditions on the marsh. Juveniles in 1971 and 1972 settled only in the marsh pans of both salt marshes. No juveniles were recorded in any of the tidal creeks, indicating that the micro-environments of the creeks may be more severe than the pans. The creeks normally drain completely on low tides and the substrate may be exposed for periods of up to 12 hours. The pans, however, seldom drain completely and are usually covered by 1 to 5 cm of water. Even though recruitment is restricted to the pans, a great deal of variability in settlement is present in these areas. Small scale differences in other physical factors such as temperature, substrate characteristics, and salinity may also affect recruitment patterns. Variability in population abundance of *Batillaria zonalis* within and between sampling localities may be the result of similar factors. Only snails larger than 3 mm are found in creeks at the 2 marshes which is probably the result of the lack of recruitment in these areas. As the snails grow, they may migrate (float) from the protected pans to the tidal creeks.

Besides being responsible for changes in the sizes of populations, unpredictable oscillations in the physical environment usually cause more flexible life history strategies (MACARTHUR & LEVINS, 1964). The number of individuals in natural populations is bound to fluctuate, but mechanisms for resisting violent fluctuations and enhancing population stability may evolve. In the present study, for example, several possible mechanisms for re-

ducing the effects of environmental fluctuations were noted. (A) During cold weather, the snails were found buried 1 to 2 cm beneath the surface of the sediment. This response may be a possible escape reaction to the wide fluctuations in temperature and rainfall that occur on the marsh during the winter months. (B) The snails are very mobile. The floating behavior was noted in all sizes of snails and represents a mechanism for easily escaping local undesirable physical or biological conditions, or both. (C) Individual snails were occasionally found cemented by glutinous threads to *Salicornia pacifica* stems 3 to 10 cm above the surface of the marsh. This behavior was primarily noted during summer months and appeared to be more common in areas of soft anaerobic substrate. This may represent a mechanism for avoiding low oxygen tensions. (D) In laboratory and field studies, the snails showed high resistance to desiccation and fluctuations in salinity.

Although salt marsh communities are characteristically species depauperate (TEAL, 1962; MACDONALD, 1967), populations inhabiting them are remarkably stable (TEAL, *op. cit.*). In the present study, aspects of the life history and biology of a salt marsh gastropod have been analyzed to ascertain the possible mechanisms which influence population regulation.

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